

Utility of Hair Structure for Taxonomic Discrimination in Bats, with an Example from the Bats of Colorado

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Hair is an important morphologic characteristic of mammals and hair identification has been used in food habit studies of predators, forensic science, textile testing, archeologic studies, and mammalian identification (Mayer, 1952; McFadden, 1968; Brunner and Coman, 1974; Appleyard, 1978; Kennedy, 1982; Valente, 1983; Oli, 1993; Wallis, 1993; Dagnall et al., 1995; Meyer et al., 1995). Hair structure in bats as well as other mammalian species has been the focus of many scientific investigations dating back to the mid 1800's (Quay 1970). However, the taxonomic importance of hair structure has been a topic of some debate. Homan and Genoways (1978), in their study of heteromyid rodents, found hair structure useful only at the generic level and not below. Similarly, Stangl and Grimes (1987) found features of the pelage useful in examining generic relationships among sciurids. Nason (1948) stated that hair structure has little taxonomic value in the identification of bats; however, Mayer (1952) found hair structure very useful in distinguishing California bats and argued that hair structure is generally species specific. Benedict (1957) also found hair structure to be a useful tool for identifying bats, particularly for categories above the species level. Dove and Peurach (2001) utilized microscopic evaluation of hair structure to determine the identity of a bat species involved in an aircraft strike. Additionally, several mammalian identification guides have included hair structure as a diagnostic character (Mayer, 1952; Benedict, 1957; Moore and Braun, 1983; Oli, 1993; Wallis, 1993).

Most studies on mammalian hair, including bat hair, were done using plastic impressions of cuticular scales and direct observation of whole mounts using light microscopy (Mayer, 1952; Benedict, 1957; Dwyer, 1962; McFadden, 1968; Brunner and Coman, 1974; Homan and Genoways, 1978; Valente, 1983; Wallis, 1993; Oli, 1993). Bower and Curry (1983) reported that scale patterns provided some of the most diagnostic characteristics for identifying hair samples, whereas Short (1978) stated that these cuticular scale patterns are only important as an accessory to other characters he considered of greater diagnostic importance. These characters included cross-sectional form and medullar form, among others. Short (1978) also pointed out that identification to species level cannot be achieved using scale form alone, but if a variety of characters are used, identification to species is possible.

Benedict (1957) and Quay (1970) classified chiropteran hair into overhair and underhair. Both described overhair as coarser, straighter, and slightly longer than the thin, wavy underhair. They noted that overhairs in bats are usually fewer in number compared to the abundance of underhair and will often exhibit a club, which is a bulb-like swelling at the distal third of the hair (Benedict, 1957; Quay, 1970). This feature also may be found at the medial region of the overhair or may be absent. Hair structure in Chiroptera is essentially uniform over the entire body with the exception of specialized areas such as glands (Benedict, 1957; Quay, 1970; Meyer et al., 1995) where scent-dispersing hairs called osmetrichia may be located. Osmetrichia differ structurally from body hair and appear to hold or disperse glandular secretions (Hickey and Fenton, 1987). Osmetrichia of some pteropodid and molossid bats differed from body hair by having more divergent cuticular scales, larger shaft diameters, and longer scale lengths as well as exhibiting some sexual dimorphism (Hickey and Fenton, 1987).

The advent of scanning electron microscopes (SEM) provided new technology that allowed for greater magnification and resolution. Several studies on bat and other mammalian hair have been conducted using this technology (Homan and Genoways, 1978; Short, 1978; Hess et al., 1985; Meyer et al., 1995).

The present study evaluated dorsal hair from 20 species of bats listed by Fitzgerald et al. (1994) that are known or expected to occur in Colorado. Two families, Molossidae and Vespertilionidae, represent the chiropteran fauna of Colorado. The molossids include

two species, Nyctinomops macrotis and Tadarida brasiliensis, and the vespertilionids comprise eight genera and 16 species, eight of which occur in the genus Myotis. Idionycteris phyllotis and Myotis velifer are species of possible occurrence and Pipistrellus subflavus has only one record of capture in the state (Fitzgerald et al., 1994).

Hairs were examined using scanning electron microscopy (SEM) and light microscopy to determine differences in hair structure. High-resolution micrographs were produced using SEM for the examination of scale form. A compound light microscope was used for the quantitative analysis of hair structure. Interspecific differences in hair structure and dimensions were used to construct a dichotomous key to the identity of Colorado chiropterans. The objective of this study was to determine if hair structure could be used as a supplemental taxonomic tool to identify the bat species of a moderate-sized geographic region in midtemperate latitudes. Keys such as this may be useful for identifying the species inhabiting different roosting sites without disturbing the bats in the roost, and also for identifying badly damaged or decomposed carcasses.

METHODS

Sample Collection.- The bats used in this study were authoritatively identified museum specimens from mammal collections housed at the University of Colorado, the Denver Museum of Natural History, and the University of Southern Colorado. Each of these twenty species was represented by three specimens except for the single specimen of *Idionycteris phyllotis*.

Hair samples were collected from the mid-dorsum at the scapular level. Hair was removed from the specimen by pinching a small tuft between the thumb and forefinger, and cutting the hair at the base as close to the skin as possible without damaging the specimen. Forceps were not used because they damaged the hairs and were awkward when working with the specimens.

Cleaning.- Methods used to clean the samples were adapted from Hess et al. (1985). Samples were

placed in a 10 ml beaker containing a solution of water and mild shampoo and sonicated in a Branson 1200 ultrasonic cleaner for five minutes. Samples were then rinsed and sonicated in dH_2O for five minutes. Samples subsequently were placed on a piece of filter paper in a petri dish and air dried for 24 hours.

Scanning Electron Microscopy.- Samples were viewed under a scanning electron microscope to obtain detailed micrographs of the hair. An International Scientific Instrument (ISI) SEM, Model SR-50, was used for this procedure. Four to six hairs from each species were fixed to aluminum mounting stubs using carbon adhesive tabs and sputtercoated with gold-palladium in an EMS-76M mini-coater for four minutes. Samples were viewed at 15 kV, and micrographs were taken at a magnification of 1320 X. Final magnification of the enlarged print was calculated by dividing the product of a measurement from the print and the

AMMAN ET AL.-- HAIR STRUCTURE OF COLORADO BATS

magnification of the negative by a measurement from the negative taken at the same place as the measurement on the print (Bozzola and Russell, 1992).

Hair Structure Analysis.– Hair characters used in this study were scale length, scale width, hair length, and scale form. Benedict's (1957) terminology was applied to describe the shape of scales along the hair. This characteristic can be diagnostically important, but it is subject to interpretation, and therefore was used in a limited capacity in this study.

Measurements of hair lengths were taken from temporary mounts under a dissecting stereoscope. Ten hairs were mounted on a glass slide using Euparal as a mounting medium. The Euparal was allowed to become tacky in order to arrange hairs horizontally to obtain accurate measurements which were taken by placing slides on a photocopy of a millimeter rule taped to a stereoscope stage. Varying magnifications were used depending on the length of hairs.

A minimum number of 10 overhairs and 10 underhairs were obtained from three specimens of each species, with the exception of *I. phyllotis* for which only one specimen was available. The minimum number of 30 hairs per species was used to establish an adequate sample size. In many cases, more than 30 hairs were used because the determination between overhair and underhair was not made until the scale measurements were taken, and if the minimum number was not reached, another slide of 10 hairs was made.

A Bausch and Lomb compound light microscope equipped with an ocular micrometer was used to measure scale length and width at the proximal, medial, and distal portions of the hair (Fig. 1) following Elgmork and Riiser (1991). Measurements of scale length were obtained by measuring the distance, in μ m, between one scale margin and the margin of the scale above or below it. The scale margin, as defined by Brunner and Coman (1974), was the free distal

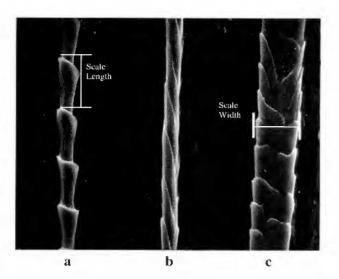


Figure 1. Electron micrograph depicting scale length and width measurements: (a) proximal, (b) medial, and (c) distal hair regions.

edge of an individual scale. Scale width was obtained by measuring the width of the scale at its widest point. Broken or worn hairs were not used in the analysis. Samples were observed using the 43X objective and the distance between ocular markings (lines) was calibrated at 1.744 μ m for 430X total magnification following Clark (1998).

Statistical Analysis.- One-way analysis of variance (ANOVA) was performed on each of the data sets for the 14 characters used in this study to determine if differences occurred among the mean values for each species. Fisher's pair-wise comparisons, set at 90 percent confidence, were performed to determine where the differences occurred. Once a difference was located, the species possessing the difference, or differences, was eligible for placement in the key. Once a species was written into the key, that species and all of its character data sets were removed from consideration, thus liberating other character data sets of remaining species. This process was carried out until all 20 species were written into the key.

RESULTS

The most notable difference among the hairs of the Colorado bats (Fig. 2) was encountered at the family level. The molossid bats, *N. macrotis* and *T. brasiliensis*, exhibit a dentate coronal scale form (Figs. 2s and 2t) while the vespertilionid bats exhibit scale forms ranging from broad lobate coronal to unequal hastate coronal, but never dentate coronal. The difference in scale form and the absence of overhair in Molossidae facilitated separation of the two families. The genus *Lasiurus* exhibited the other readily distinguishable scale form, described as slightly divergent lobate to broad lobate (Figs. 2g and 2h).

A more general observation was that scale lengths are usually greatest at the proximal segment of the hair and, decrease as scale width increases at the medial and distal segments. With overhair, the shortest scales are usually associated with the club. Scale measurements and hair lengths are listed in Table 1.

A dichotomous key to the bats of Colorado using the external morphology of dorsal hair was produced (Appendix I). Five species had character values that did not overlap with any other character value, and in addition to unique scale forms, were used to initiate the construction of the key. These include: mean hair length underhair for I. phyllotis; mean hair length underhair for T. brasiliensis; mean scale width medial overhair for Antrozous pallidus; mean scale length medial and proximal overhair for Lasiurus cinereus; mean scale width medial overhair for Myotis volans; and mean scale width distal and medial underhair for T. brasiliensis (Table 1). The key was designed to be used with sample sizes of 30 or more overhairs and underhairs and is primarily quantitative in nature to avoid the subjectivity inherent in the description of scale form. Not all hairs will fit the classic definitions of overhair and underhair and misidentification of such hairs may cause erroneous results. This key also was designed to be used as a supplemental taxonomic tool, and we caution that identification to the species level should always be made with other morphologic and geographic qualifications. Micrographs of dorsal hair scale form (Fig. 2) are of the distal portion of the overhair for most of the species; however, some represent distal underhair and are labeled accordingly. All measurements are listed with 90 percent confidence intervals.

DISCUSSION

Scale form, although diagnostically important, was used sparingly in this study. The two families investigated were easily distinguished using scale form as the determining factor. In agreement with Benedict (1957), molossid bats had a scale form classified as divergent to divericate, dentate coronal. *Lasiurus* also was discernable from other Colorado species using a scale form described as lobate to broad lobate coronal. The scope of the study centered on the quantitative analysis of hair structure in an attempt to provide a more objective and thorough method of differentiating the species.

Mayer's (1952) study on the hair of California mammals included vespertilionids and molossids; much of his key was based on hair color and maximum measurement values. There was no mention of the number of hairs used other than the indication that some mammalian species required the use of numerous samples. Comparisons of our findings with those of Mayer (1952) show some discrepancies. For example, Mayer (1952), lists the maximum hair length of *A. pallidus* overhair as 8.0 mm whereas our findings show the maximum hair length for overhair was 11.5 mm with the mean hair length of 8.04 mm.

Maximum hair lengths for *Eptesicus fuscus* and *Euderma maculatum* were 10.0 mm and 12.5 mm respectively, which were greater than Mayer's (1952) observation by 2.0 mm and 2.5 mm respectively. Benedict (1957) lists the maximum hair length of the single *E. maculatum* examined in her study at 15.0 mm, which is much greater than our value. Our mean scale measurements for *E. maculatum* were similar, however, despite the discrepancy in the number of specimens examined.

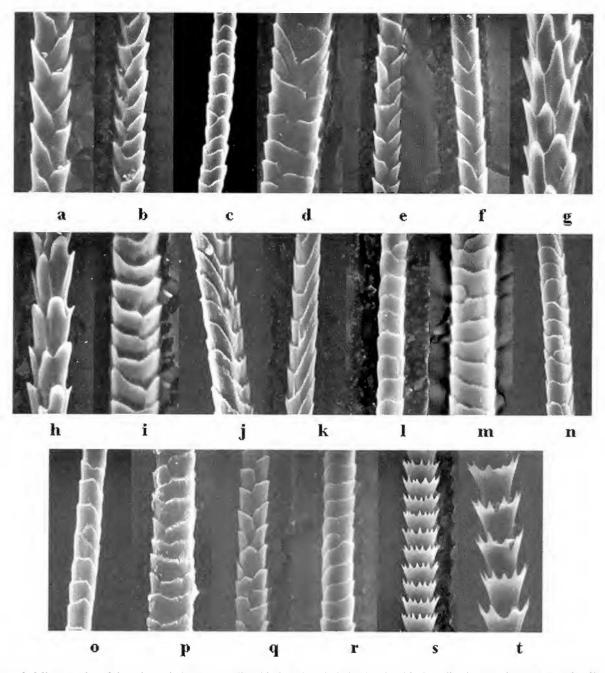


Figure 2. Micrographs of dorsal overhairs (Vespertilionidae) and underhairs (Molossidae). All micrographs represent the distal portion at a magnification of 1320 X: a) *Antrozous pallidus*, b) *Corynorhinus townsendii*, c) *Eptesicus fuscus*, d) *Euderma maculatum*, e) *Idionycteris phyllotis*, f) *Lasionycteris noctivagans*, g) *Lasiurus borealis*, h) *Lasiurus cinereus* (underhair), i) *Myotis californicus*, j) *Myotis ciliolabrum*, k) *Myotis evotis*, 1) *Myotis lucifigus*, m) *Myotis thysanodes*, n) *Myotis velifer*, o) *Myotis volans*, p) *Myotis yumanensis*, q) *Pipistrellus hesperus*, t) *Pipistrellus subflavus*, s) *Nyctinomops macrotis* (underhair), t) *Tadarida brasiliensis* (underhair).

		Overl	nair	Unde	rhair	
Species		scale length	scale width	scale length	scale width	
A. pallidus	Distal	12.18	15.70	12.08	11.78	
P	Medial	15.45	12.43	15.40	13.14	
	Proximal	19.50	12.12	20.04	13.10	
	Hair length	8.04	12.12	7.32	15110	
					4.9. 6.9	
C. townsendii	Distal	8.02	14.20	7.97	10.60	
	Medial	11.64	8.79	10.18	10.89	
	Proximal Unit langth	14.16	11.13	14.38	11.12	
	Hair length	10.96		8.68		
E. fuscus	Distal	6.78	13.53	7.16	9.24	
	Medial	10.30	9.56	10.23	9.71	
	Proximal	14.28	9.04	14.0	9.29	
	Hair length	7.69		6.61		
E	Distal	0.25	15.70	8.93	9.97	
E. maculatum	Distal Medial	8.35 11.02	15.70	8.93 11.46	10.55	
			10.71	13.25	9.51	
	Proximal Hair length	13.06 9.84	10.13	7.10	ي د. ج	
	man tengtu	2.04		7.10		
I. phyllotis	Distal	7.54	13.18	7.33	9.36	
	Medial	11.49	8.92	9.88	10.12	
	Proximal	16.41	10.46	15.64	10.06	
	Hair length	10.88		9.42		
	Distal	7.95	13.18	8.09	9.35	
L. noctivagans			9.18	11.43	10.20	
	Medial	11.88	10.26	17.07	9.54	
	Proximal Hair length	18.33 8.66	10.20	7.13	2.54	
	man length	0.00				
L. borealis	Distal	13.82	13.82	13.75	9.12	
	Medial	17.57	9.55	17.91	9.93	
	Proximal	20.75	11.07	21.16	12.17	
	Hair length	9.38		8.57		
L. cinereus	Distal	14.10	15.99	14.16	9.61	
E. Chiereus	Medial	20.10	10.17	19.83	9.86	
	Proximal	22.14	12.50	21.01	11.36	
	Hair length	9.45		8.82		
			14.00	7.45	0.24	
M. californicus	Distal	7.95	14.93	7.65	9.24	
	Medial	15.44	9.74	14.82	10.03	
	Proximal	19.40	10.46	19.06 6.02	10.34	
	Hair length	7.62		0.02		
M. ciliolabrum	Distal	7.89	14.78	7.83	9.20	
	Medial	9.77	9.24	10.33	9.44	
	Proximal	18.57	10.86	18.23	10.22	
	Hair length	7.22		6.16		
				0 70	9.47	
M. evotis	Distal	9.49	14.57	8.79	9.47	
	Medial	12.46	10.00	11.83		
	Proximal Unit longth	20.11 8.87	10.57	19.76 7.63	10.67	
	Hair length	0.07		7.00		
M. lucifugus	Distal	8.95	15.04	7.94	9.24	
,	Medial	17.40	8.99	17.22	9.46	
	Proximal	20.15	11.08	19.56	10.46	
	Hair length	8.12		6.54		

AMMAN ET AL.--- HAIR STRUCTURE OF COLORADO BATS

Table 1 cont'd.

		Overh		Unde		
Species		scale length	scale width	scale length	scale width	
M. thysanodes	Distal	8.36	13.99	8.12	9.06	
	Medial	11.11	10.02	10.97	9.70	
	Proximal	18.29	10.67	18.72	10.21	
	Hair length	7.37		6.02		
M. velifer	Distal	8.34	16.12	8.13	9.74	
	Medial	11.37	9.99	11.71	10.23	
	Proximal	17.53	10.60	18.72	9.71	
	Hair length	7.64		6.19		
M. volans	Distal	7.21	12.94	7.32	8.20	
	Medial	9.77	8.10	9.42	8.58	
	Proximal	17.79	9.22	18.07	9.00	
	Hair length	7.92		6.99		
M. yumanensis	Distal	8.67	13.16	8.48	9.40	
	Medial	11.16	9.02	11.04	9.44	
	Proximal	18.64	10.51	19.18	10.19	
	Hair length	6.53		6.25		
P. hesperus	Distal	8.52	13.44	9.10	9.24	
	Medial	12.89	9.51	12.30	9.38	
	Proximal	16.79	9.92	16.45	10.09	
	Hair length	6.03		5.18		
P. subflavus	Distal	7.54	12.77	7.88	8.54	
	Medial	11.64	9.56	12.35	9.08	
	Proximal	18.12	9.45	19.04	9.34	
	Hair length	5.90		5.37		
N. macrotis	Distal			6.83	12.43	
	Medial			10.54	14.66	
	Proximal			14.58	16.03	
	Hair length			6.21		
T. brasiliensis	Distal			11.92	16.50	
2. 0. 00000000	Medial			16.42	16.20	
	Proximal			19.62	16.42	
	Hair length			4.49		
F values	Distal	103.29***	11.04***	112.77***	66.02***	
	Medial	58.50***	12.08***	88.07***	63.47***	
	Proximal	49.64***	13.48***	46.16***	69.55***	
	Hair length	56.62***			73.12***	

Our hair length measurements of *Lasionycteris* noctivagans, 11.2 mm, were consistent with Benedict (1957), 11.0 mm, but our mean scale length and width measurements were different. Benedict recorded a mean scale length medial overhair of 13.6 μ m and a mean scale width medial overhair of 11.9 μ m compared to our findings of 11.88 μ m for scale length medial overhair. The differences observed between our study and those of Benedict (1957) and Mayer (1952) may be reflective of many things including methodology, number of specimens and samples examined, geographic variation of the samples, and differences in technology.

We believe that hair structure can be a useful taxonomic character, as shown in Appendix 1, to distinguish among a moderate number of species, including congeneric species, even though it has been used as a generic character for bats in the past (Benedict, 1957). Modern technology such as the SEM and statistical software were also essential in making determinations of difference between species that may have been overlooked otherwise. Areas of the hair such as the proximal portion that were deemed unusable in the past (Benedict, 1957) have been proven useful for the identification of Colorado bat species; the mean scale length of the proximal portion of the overhair of L. cinereus (Table 1) is an example. The fact that this study involved a limited number of species from a limited geographic area facilitated the demarcation of species based on external hair morphology. Mean values from measurements taken on numerous samples were used providing a more accurate representation of the scale dimensions of the species of Colorado bats.

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AMMAN ET AL.— HAIR STRUCTURE OF COLORADO BATS

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APPENDIX I.

Key To Colorado Chiroptera Species Using Dorsal Hair Characteristics

* Sp	becies of possible occurrence in Colorado. All measurements are listed with their 90% confidence intervals.
la.	Scale form divergent to divericate, dentate coronal; overhair and underhair are not discernible (Figs. 2s and 2t). Family Molossidae
lb.	Scale form not as above; overhair and underhair are discernable. Family Vespertilionidae
2a.	Mean hair length of 4.49 ± 0.10 mm; mean scale width distal underhair of $16.50 \pm 0.40 \mu$ m; mean scale width medial underhair of $16.20 \pm 0.52 \mu$ m (Fig. 2t) Brazilian free-tailed bat - <i>Tadarida brasiliensis</i>
2b.	Mean hair length 6.21 \pm 0.27 mm, mean scale width distal underhair of 12.43 \pm 0.43 μ m; mean scale width medial underhair of 14.66 \pm 0.48 μ m; mean scale width proximal underhair of 16.03 \pm 0.58 μ m (Fig. 2s)
3a.	Scale form slightly divergent, lobate to broad lobate coronal distally becoming mixed with equal hastate medially (Figs. 2g and 2h). Lasiurus
3b.	Scale form not as above
4a.	Mean scale length medial overhair of $20.10 \pm 0.92 \ \mu m$; mean scale length proximal overhair of $22.14 \pm 0.95 \ \mu m$; mean scale length medial underhair of $19.83 \pm 1.06 \ \mu m$ (Fig. 2h) Hoary bat - <i>Lasiurus cinereus</i>
4b.	Mean scale length medial overhair of $17.57 \pm 0.69\mu$ m; mean scale length proximal overhair of $20.75 \pm 0.77 \mu$ m; mean scale length medial underhair of $17.91 \pm 0.41 \mu$ m; mean scale width proximal underhair of $12.17 \pm 0.44 \mu$ m; mean hair length overhair of 9.38 ± 0.25 mm; mean scale length distal overhair of $13.82 \pm 0.53 \mu$ m (Fig. 2g)
5a.	Mean scale length distal overhair of $12.18 \pm 0.40 \ \mu\text{m}$; mean scale length distal underhair of $12.08 \pm 0.42 \ \mu\text{m}$; mean scale width medial overhair of $12.12 \pm 0.36 \ \mu\text{m}$; mean scale width distal underhair of $11.78 \pm 0.48 \ \mu\text{m}$; mean scale width medial underhair of $13.14 \pm 0.57 \ \mu\text{m}$; mean scale width proximal underhair of $13.10 \pm 0.52 \ \mu\text{m}$ (Fig. 2a)
5b.	Mean scale dimensions not as above 6
6a.	Mean hair length underhair of 9.42 ± 0.35 mm (Fig. 2e) Allen's big-eared bat - Idionycteris phyllotis*
6b.	Mean hair length underhair less than 9.08 mm7

AMMAN ET AL.— HAIR STRUCTURE OF COLORADO BATS

Appendix I (continued).

7a.	Mean hair length overhair of 10.96 ± 0.46 mm; mean hair length underhair of 8.68 ± 0.35 mm; mean scale width distal underhair of $10.60 \pm 0.43 \ \mu m$ (Fig. 2b)
7b.	Mean hair length overhair less than 10.50 mm; mean hair length underhair less than 8.34 mm; mean scale width distal underhair not as above
8a.	Mean hair length overhair of 9.84 \pm 0.37 mm; mean scale length proximal overhair of 13.06 \pm 0.29 μ m; mean scale width medial overhair of 10.71 \pm 0.42 μ m (Fig. 2d)
8b.	Mean hair length overhair less than 9.47 mm; mean scale length proximal overhair greater than 13.36 μ m; mean scale width medial overhair not as above
9a.	Mean scale length proximal overhair of $14.28 \pm 0.67 \ \mu$ m; mean scale length proximal underhair of $14.0 \pm 0.62 \ \mu$ m (Fig. 2c)
9b.	Mean scale length proximal overhair and underhair not as above 10
10a.	Mean scale length distal overhair of 9.49 \pm 0.42 μ m; mean scale width distal overhair of 14.57 \pm 0.54 μ m (Fig. 2k) Long-eared myotis - <i>Myotis evotis</i> .
10b.	Mean scale length and width distal overhair not as above 11
11a.	Mean scale width medial overhair of $8.10 \pm 0.30 \ \mu\text{m}$; mean scale length medial underhair of $9.42 \pm 0.39 \ \mu\text{m}$ (Fig. 20) Long-legged myotis - <i>Myotis volans</i>
116.	Mean scale width medial overhair greater than 8.40 μ m; mean scale length medial underhair not as above
12a.	Mean hair length overhair of 8.12 ± 0.20 mm; mean hair length underhair of 6.54 ± 0.19 mm; mean scale length medial overhair of $17.40 \pm 1.06 \mu$ m; mean scale length medial underhair of $17.22 \pm 0.92 \mu$ m (Fig. 21)
12b.	Mean hair length overhair and underhair and mean scale length medial overhair and underhair not as above
13a.	Mean scale length medial overhair of $15.44 \pm 0.89 \ \mu m$; mean scale length medial underhair of $14.82 \pm 0.64 \ \mu m$ (Fig. 2i)
13b.	Mean scale length medial overhair and underhair not as above14

Appendix I (continued).	

4a.	Mean scale length medial overhair of 9.766 \pm 0.432 μ m; mean scale width distal overhair of 14.780 \pm 0.557 μ m
	(Fig. 2j)
4b.	Mean scale length medial overhair and mean scale width distal overhair not as above
5a.	Mean scale width distal overhair of $16.12 \pm 0.94 \mu\text{m}$ (Fig. 2n) Cave myotis - <i>Myotis velifer</i> *
5b.	Mean scale width distal overhair less than 15.18 μ m
6a.	Mean hair length overhair of 7.37 ± 0.31 mm (Fig. 2m) Fringed myotis - <i>Myotis thysanodes</i>
6b.	Mean hair length overhair not as above 17
7a.	Mean hair length underhair of 6.25 ± 0.20mm (Fig. 2p) Yuma myotis - Myotis yumanensis
7b.	Mean hair length underhair not as above 18
8a.	Mean hair length overhair of 8.66 ± 0.42 mm; mean hair length underhair of 7.13 ± 0.22 mm (Fig. 2f)